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AN ECOLOGICAL AND BEHAVIORAL STUDY OF THE AYE-AYE (*Daubentonia madagascariensis*)

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ABSTRACT This report forms one of a series of papers examining my hypothesis that the aye-aye's (*Daubentonia madagascariensis*) unusual adaptation is more reasonably explained by a diet of hard-nuts rather than one of wood-boring insect larvae.

An extensive survey showed that the distribution of the aye-aye and that of *Canarium* spp. (which bears hard-nuts) overlapped on the eastern coast and in the central highland of Madagascar.

An intensive study was conducted at the Nosy Mangabe Special Reserve on a total of 33 nights during three different periods in 1988 and 1989. I observed the aye-ayes eating ramy nuts (*Canarium* spp.) throughout the entire observation period, the parasitical outgrowth of the cambial layer of *Afzelia bijuga* from June through October except for August, insect larvae, beans of *Entada phaseoloides*, and the flowers of *Macaranga cuspidata* from September to October.

The aye-aye spends a relatively high proportion (over 40%) of its time engaged in feeding during October and December when ramy forms the main part of its diet, while from June to July, and September, when other food items are additionally consumed, the proportion of resting time becomes relatively high (over 10%).

Although the aye-aye was often spotted singly, it was also common to see more than one individual (up to four) adjacent to another (13% of all the observation units in which the aye-aye was spotted) throughout the observation periods.

Two species of ramy (*Canarium* spp.) are distributed in the Nosy Mangabe Special Reserve. *C. Boivini* bore fruits over the entire observation period. A single nut of the ramy provides of 4.38 kcal of energy and requires about two minutes on average for consumption. I estimated the nightly energy intake as 262.8 kcal.

Key Words: Aye-aye; *Daubentonia madagascariensis*; Feeding behavior; *Canarium* spp.; *Afzelia bijuga*; Hard-nut adaptation hypothesis.

INTRODUCTION

When the aye-aye was discovered, no ecological observations were reported because, as described by Sandwith in his letter to Owen (1983), the native inhabitants often believed that the aye-aye (called "hai-hai" by local people) was an incarnation of "fady" (evil spirits). My survey also found that the consumption of aye-ayes has been regarded to date as taboo and prohibited in districts on the east coast such as Maroantsetra, Antalaha and Mananala, although in the northern part of the central highland near Mandritsara and Befandriana Nord, where the people have recently become accustomed to eating aye-ayes. It is said that whenever a local inhabitant sees an aye-aye in the daytime, he kills it because it is

supposed to bring misfortune. Thus, it is still difficult to gather information on the living state of the aye-ayes from the local people. A field survey on the aye-aye was launched by Petter et al. in 1957 (Petter & Petter-Rousseax, 1959; Petter & Peyrieras, 1970; Petter, 1977; Petter et al., 1977), but their survey covered all prosimian groups and was not restricted to the aye-aye. The aye-aye's nocturnal activity and the scant information available from local inhabitants have severely limited study of the aye-aye.

Less than 10 studies on the aye-aye were reported during the 1980s including my own, and most were only fragmentary (Bomford, 1981; Kemf, 1983; Constable et al., 1985; Pollock et al., 1985; Ganzhorn & Rabesoa, 1986; O'Connor et al., 1987; Iwano & Iwakawa, 1988; Wilson et al., 1989). The data, in short, consisted only of records of the location of aye-aye observations.

Iwano & Iwakawa (1988) reported for the first time that the aye-aye fed on nuts of ramy (*Canarium* spp.), a plant indigenous to Madagascar. Based on this finding, we proposed an alteration to the previously advocated woodpecker hypothesis (Cartmill, 1974) regarding the ecological niche of the aye-aye. The woodpecker hypothesis related the unusual morphological characteristics of the aye-aye to its feeding behavior. The combined function of its continuously growing chisel-like incisors and its narrowed third digit have drawn the attention of many researchers since their discovery. Cartmill suggested that these two peculiar morphological traits represented an adaptation for the extraction of wood-boring insect larvae, thus permitting the aye-aye to fill the ecological niche normally filled by woodpeckers, which are absent form Madagascar.

Our new hypothesis is based on the following three points:

(1) The continuously growing incisors and the slender third digit of the aye-aye are indispensable tools, for feeding on ramy nuts, which have very hard shells, and whose contents are divided into three small compartments, in an efficient way.

(2) The aye-aye is exceptionally large (3 kg) compared with other insectivorous primates (0.06–0.2 kg) and it is unlikely that it could depend upon insects as a major food source.

(3) There are two kinds of birds that prey on the wood-boring insect larvae on Madagascar (Petter, 1977). Accordingly, the ecological niche to feed on the wood-boring insect larvae is already filled by these birds. On the other hand, the niche to feed on hard-nuts is exclusively occupied by the aye-aye, since squirrels are absent from Madagascar (Petter, 1972).

The hypothesis suggests a number of questions: How is the ramy distributed in Madagascar? How do the distributions of the ramy and the aye-aye overlap? Is the ramy nut truly the staple food of the aye-aye? When does the ramy bear fruit in the area where the aye-aye lives? What does the aye-aye eat when the ramy does not bear fruit?

This study was undertaken with the aim of searching for the answers to these questions by elucidating the ecology of the aye-aye, and to test the validity of the hard-nut adaptation hypothesis.

METHODS

A survey of the distribution of ramy trees was carried out in the forested district of the eastern coast and the northern district of the central highland of Madagascar from November to December 1988, and in August 1989. In the survey, I selected several study sites between 15°29' S and 25°S, to get a general view of the distribution of the aye-aye and the ramy.

The ecology of the aye-aye was studied at the Nosy Mangabe Special Reserve, and included a survey of the seasonal changes in fruiting of the ramy (*Canarium* spp.). The ecological study of the aye-aye was conducted in December 1988, from June to July 1989 and from September to October 1989. The phenological study on the fruiting of the ramy was conducted between June 1989 and June 1990.

The research team, consisting of two to six members, searched predetermined routes in the mountainous region along the southwest coast of Nosy Mangabe and, on alternate nights, along the beach, every night (from 18:00 hrs till 5:00 hrs the next day), and followed the aye-aye whenever it was discovered. We used a beam light of 150,000 lux (12 V) and torches (3–6 V).

The observation period at night was divided into units of one minute duration and the activity of the aye-aye in each unit was recorded. The activity categories were as follows.

(1) Activity: feeding, moving, resting, grooming, vocalization, and social behavior.
   (a) Feeding: It was often difficult to observe the aye-ayes putting something into their mouths because they fed in thickets within the canopy about 20 m above the observers, or faced the tree trunks with their backs toward the observers when they fed on *Afzelia bijuga*. Therefore, eating was identified through a number of indirect methods: the aye-aye generated rather loud, characteristic sounds when gnawing on the shell of ramy nuts, and the shell fragments made sounds upon falling (both for ramy and *A. bijuga*). Handling time, including the time spent peeling off the shell or the bark and gnawing a hole, was scored under the category of feeding.
   (b) Moving: When the aye-aye was observed to move.
   (c) Resting: When the aye-aye was observed to be immobile.
   (d) Grooming: When the aye-aye was observed to lick or rub its body with its mouth, hands or feet.
   (e) Vocalization: When aye-aye calls were heard, they were recorded separately from other behaviors. Whether or not the call was generated by an individual under observation was noted. I could discern two kinds of characteristic vocalizations.
   (f) Social behavior: When more than one individual was observed to be engaged in interactions, such as charging or chasing, etc. More than one individual sitting side by side without apparent interaction was not treated as social behavior.
(2) Foods: names and parts eaten.
(3) Number of fallen nuts.
(4) Other remarks: location (tree trunk, branch, crown and ground), height (over

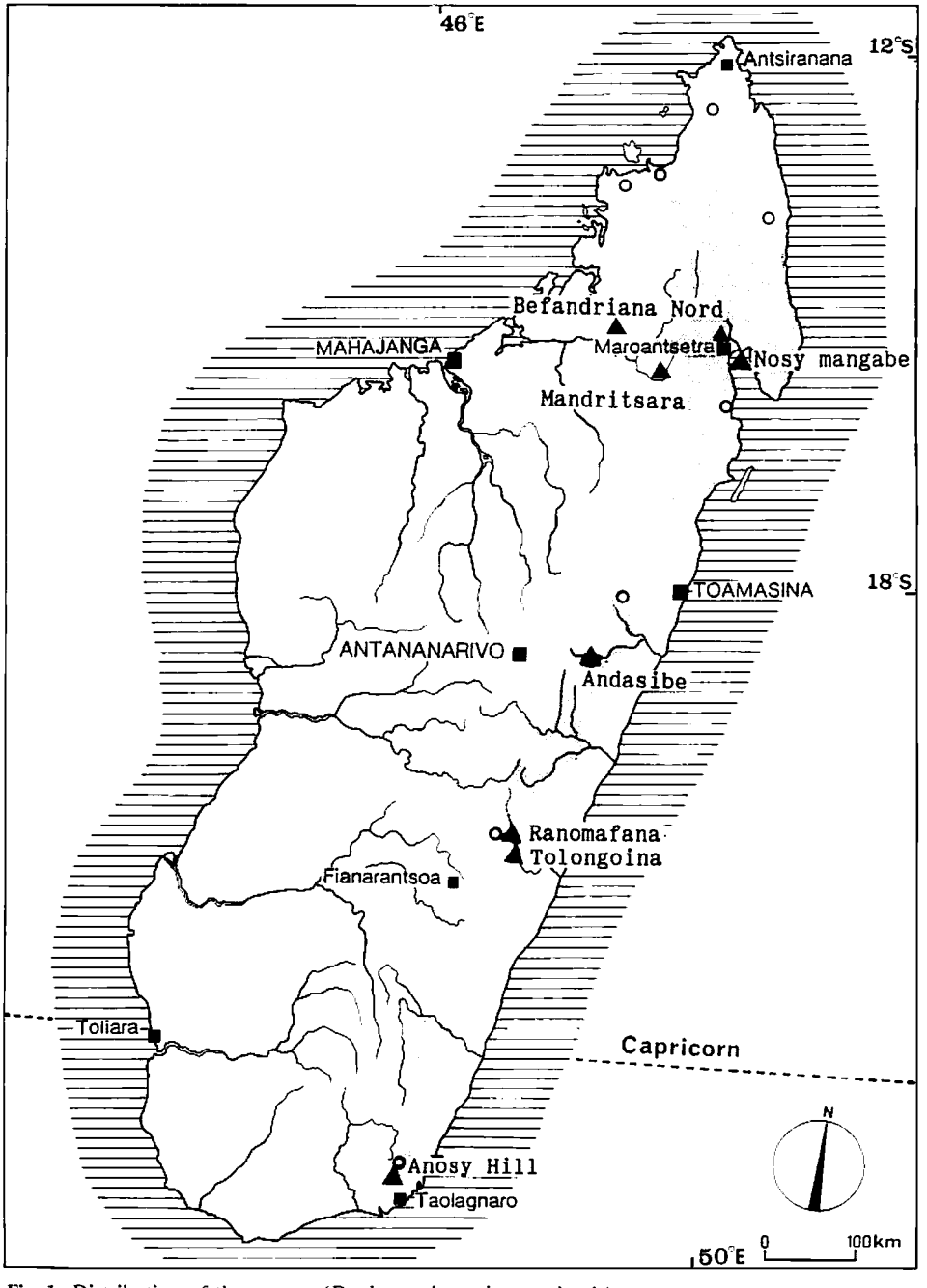

Fig. 1. Distribution of the aye-aye (*Daubentonia madagascariensis*).
▲: Existence of the aye-aye (present study); ○: Information of the aye-aye (literature); ■: Major city; ⊡: Rain forest.

25 m, between 25 and 10 m, and less than 10 m).

The seasonal abundance of the ramy nut was studied twice a month in tree samples (46 for *C. madagascariense* and 1 for *C. Boivini*), and the total number of ramy trees that bore fruit within the study area were counted.

STUDY SITE

In the survey on the distribution of the aye-aye and ramy, I selected several study sites between Maroantsetra (15°29'S) and Tolanaro (25°S) in the eastern coast and around Befandriana Nord (15°15'S) in the northern part of the central highland (Fig.1).

There are no official records of weather at Maroantsetra. However, the data for Toamasina (18°9'S) and Vohemar (13°22'S) (from Fig. 2 in Donque, 1972), indicated that the maximum average temperature (26°C) is in February and the minimum (22.5°C) falls in July to August with only a 3.5°C difference between the two.

The region near Antongil Bay receives the most precipitation in Madagascar, 350 mm per month on average (Donque, 1972). The rainy season starts in December and continues until March. Even after April, however, the region often receives heavy rains through to July. The region is comparatively free from rain from August to November.

At Nosy Mangabe Special Reserve, the lowest average monthly temperature was recorded in June, although observations began in the latter half of that month (Table 1). The daily weather was entered only as a reference because the weather changed so drastically that it was practically impossible to include it under a single heading.

I selected Nosy Mangabe Special Reserve for the ecological study of the aye-aye. Nosy Mangabe (15°29'S and 49°45'E, 520 ha and 331 m above sea level at its highest point) is a small island uninhabited by people, located in a corner of Antongil Bay on the eastern coast of Madagascar. Its entire area was designated as a special reserve in 1966 and nine aye-ayes were released on the island in 1967 (Petter, 1977).

A description of its vegetation has been given elsewhere (Iwano & Iwakawa, 1988). Two species of ramy grow in Nosy Mangabe, *C. Boivini* from the coast to about 200 m above sea level and *C. madagascariense* in areas over 100 m above sea

Table 1. Temperature and weather at Nosy Mangabe from June to December, 1989.

Month	Temperature C			Weather: Days & %( )			Observation
	Max.	Min	Ave.	Fine	Cloudy	Rain	Days
June	21.8	19.7	20.8	2(14.3)	9(64.3)	3(21.4)	14
July	24.4	18.8	22.2	7(24.1)	16(55.2)	6(20.7)	29
August	23.7	18.5	21.3	9(29.0)	19(61.3)	3(9.7)	31
September	24.3	19.4	22.4	7(25.0)	20(71.4)	1(3.6)	28
October	33.0	18.5	24.3	17(68.0)	7(28.0)	1(4.0)	25
November	35.0	19.7	25.3	18(66.7)	9(33.3)	0(0.0)	27
December	34.0	21.2	26.2	15(50.0)	9(30.0)	6(20.0)	30

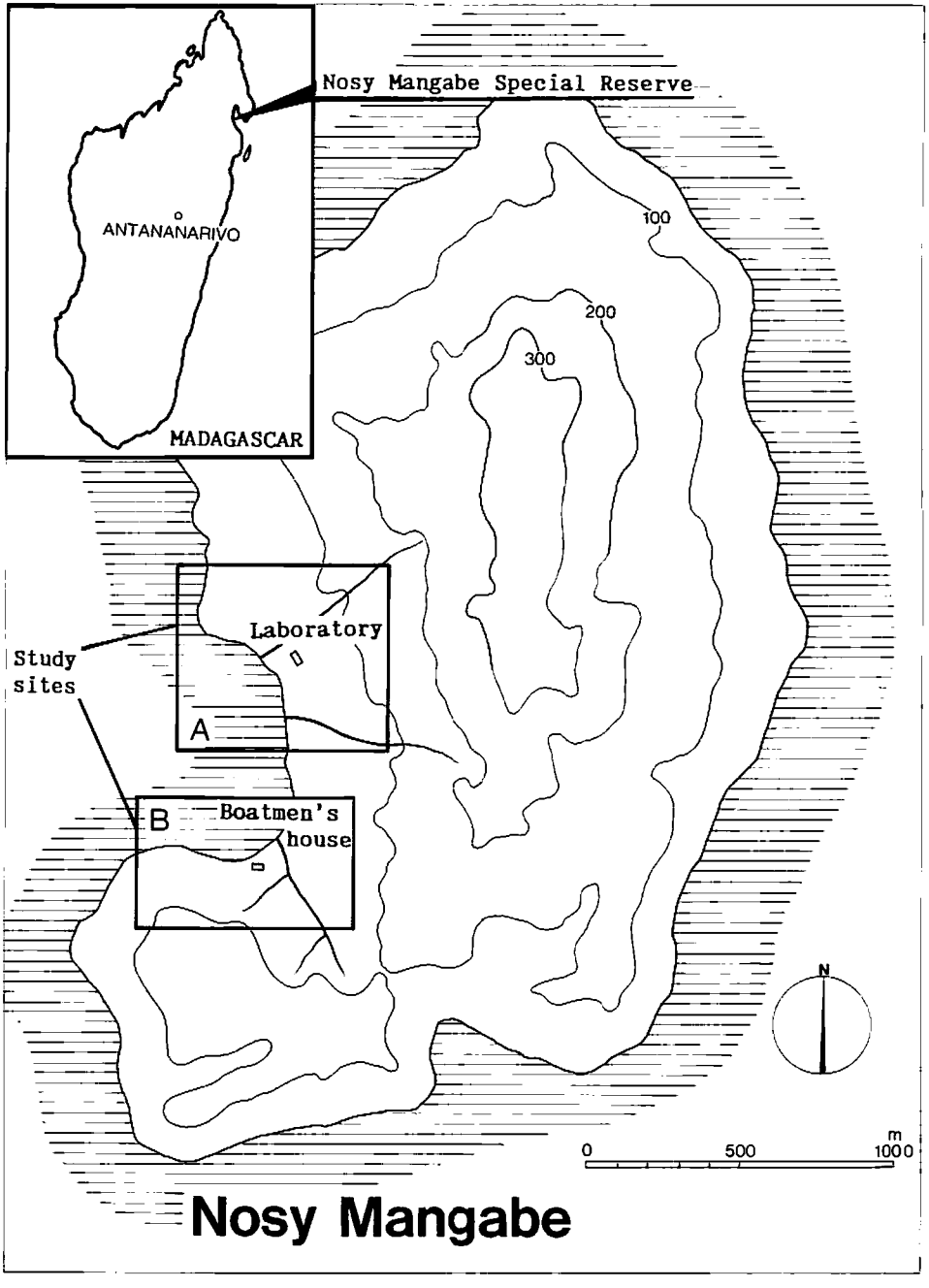

Fig. 2. Area chosen for the ecological study of the aye-aye (*Daubentonia madagascariensis*).

level. Thus, *C. Boivini* appears to be the dominant species in Nosy Mangabe. *A. bijuga* grows from the coast to less than 75 m above sea level. I chose two study sites along the western coast of the island (Fig. 2). The land around Antongil Bay mainly consists of granite cliffs more than 150 m high (Battistini, 1972). Nosy Mangabe island is also composed of granite and has steep slopes around it.

RESULTS

I. Distribution

The data concerning the sightings of the aye-aye on the eastern coast can be summarized as follows: aye-ayes were observed at Nosy Mangabe, Andasibe, and Ranomafana; tooth marks on *Afzelia bijuga* trees and three nests were found in Maroantsetra; feeding traces on ramy nuts were found in Tolongoina and Anosy hills. In these places, I found two species of the ramy (*C. Boivini* and *C. madagascariense*).

In the central highland, I confirmed the existence of the aye-aye at Befandriana Nord from tooth-marks, feeding traces on ramy nuts, and five nests. Mr. H. Fukazawa collected the tail of an aye-aye which had been eaten by local people at Mandritsara. In these districts, forests are predominantly ramy (*C. madagascariense*) and mango trees along the rivers.

The ramy flourishing at Befandriana Nord is called "haramy", and its fruiting season has been said to fall between March and May by the local people. However, I saw that they bore fruits even in August.

Table 2. Food items consumed by aye-ayes and observation samples from December 1988 to October 1989.

FAMILY Species (Vernacular)	Part eaten	1988	1989			Total	Percentage
		Dec.	Jun.—Jul.	Sept.	Oct.		
BURSERACEAE							
Canarium Boivini	Nut	354	+	152	109	615	(60.2)
(Ramy)	Bark	3	−	−	−	3	(0.3)
C. madagascariense (Ramy/Haramy)	Nut	−	+	+	+		
LEGUMINOSAE							
Afzelia bijuga (Hintsina)	Bark	−	142	214	−	356	(34.9)
Entada phaseoloides (Voankarabo)	Bean	−	−	1	−	1	(0.1)
EUPHORBIACEAE							
Macaranga cuspidata (Mongy)	Nectar	−	−	32	−	32	(3.1)
INSECT LARVAE	Body	−	+	14	+	14	(1.4)
Total		357	142	413	109	1,021	(100.0)

+: Feeding tracks.
−: Not observed and no feeding track.

II. Diet

The diet of the aye-aye was found to include five kinds of plants (including two species of *Canarium*), and a number of wood-boring larvae, though their genera could not be identified (Table 2).

The aye-aye's feeding sequence on ramy nuts consisted of four steps: (1) searching for a fruit; (2) holding the fruit and settling down; (3) scraping the pulp and gnawing into the hard shell of the nut, and (4) extracting and eating the contents.

Aye-ayes ate the interior of the bark or the cambial layer of *A. bijuga* (referred to as "bark" hereafter) during the surveys of June to July and September to October. When feeding on *A. bijuga*, the aye-aye peeled off the bark and ate the underlying cambial layer, releasing a sweet odor by scooping it out with the lower incisors (Fig. 3).

I observed aye-ayes feeding on the flowers of *Macaranga cuspidata* and *Entada phaseoloides*. It is likely that aye-ayes eat the nectar or pollen of the flowers. They also feed on the large beans of the latter species.

In each survey period, I saw feeding marks on dead trees throughout the study area, possibly left by aye-ayes searching for wood-boring larvae. In the survey lasting from September to October, I observed aye-ayes eating larvae after tearing open the bark of a branch with their teeth.

I saw aye-ayes feeding on ramy nuts throughout the survey periods. Although I did not directly observe aye-ayes feeding on ramy nuts from June to July 1989, I

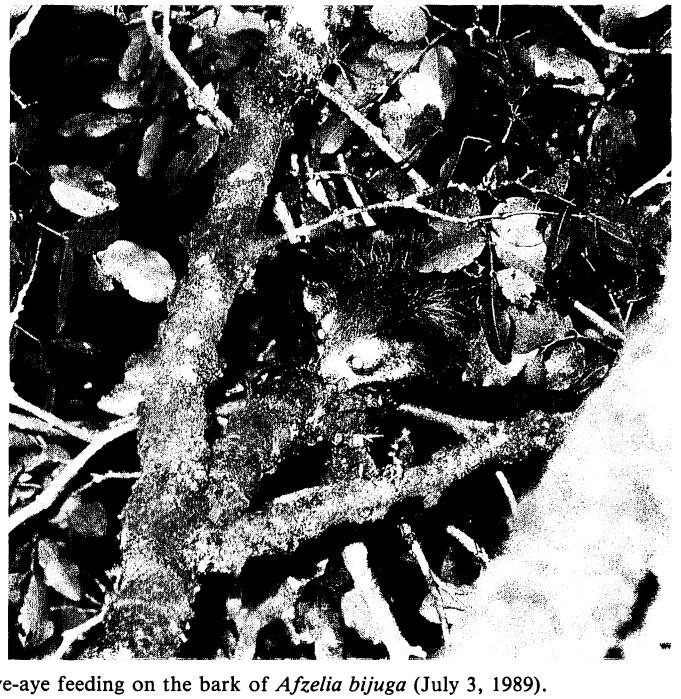

Fig. 3. The aye-aye feeding on the bark of *Afzelia bijuga* (July 3, 1989).

could detect new feeding marks on some ramy nut shells. This period coincided with a time when aye-ayes mainly consumed *A. bijuga*. In the survey from September to October, I could not see aye-ayes feeding on ramy until late September. *Macaranga cuspidata* and *Entada phaseoloides* were observed to be the diet of the aye-aye only in September and October. Although the changes in the aye-aye's diet seem to be drastic, it might be mainly due to the fragmental nature of my data. Therefore, more detailed observation is needed to examine the seasonal changes of their diet.

III. Feeding Behavior

Feeding time for individual food items were totaled for each hour of the evening when aye-ayes' activity was observed (Table 3). Aye-aye's feeding time varied depending on the food item eaten. *A. bijuga* was eaten most frequently between 18:00 and 22:00 hrs (91% of the total observation units at which *A. bijuga* was found to be eaten), ramy, most often between 22:00 and 0:00 hrs (72.5%), and *E. phaseoloides* beans and insect larvae, before 22:00 hrs.

The longest feeding time for ramy was 111 minutes with an average of 59 minutes (S.D.=32.0, N=12). Feeding times for *A. bijuga* ranked second in duration, the longest time being 60 minutes. The average duration was 29.4 minutes (S.D.=25.3, N=14). For the calculation of the average, I excluded those cases in which feeding on *A. bijuga* lasted for less than one minute.

Feeding on the flowers of *M. cuspidata* was observed four times with the longest duration being 22 minutes. Feeding on insect larvae was observed four times with the longest duration being nine minutes. I observed aye-ayes feeding on the beans of *M. cuspidata* only once with a duration of one minute.

I could deduce the rate at which an aye-aye ate ramy nuts from the sounds generated by falling nuts discarded by the aye-aye engaged in feeding, and had 11 opportunities for such measurements (total duration being 496 minutes). The time an aye-aye required for consuming a ramy nut was 126 seconds on average (S.D.=0.5, N=11). This value is slightly larger than the equivalents in the previous study conducted in December 1984 (102 seconds), or under artificial

Table 3. Observation samples of feeding by aye-ayes in each hour for ramy and other food items in 1988 and 1989.

Food items	Month	Hour											Total
		18	19	20	21	22	23	0	1	2	3	4	
Canarium nut	Dec.	1	2	18	14	136	74	16	42	30	20	1	354
	Sep.	0	0	0	41	0	54	57	0	0	0	0	152
	Oct.	0	0	0	0	25	41	43	0	0	0	0	109
Canarium bark	Dec.	0	0	1	2	0	0	0	0	0	0	0	3
Afzelia bark	Jun.—Jul.	0	0	13	78	51	0	0	0	0	0	0	142
	Sep.	28	91	47	4	12	25	1	0	6	0	0	214
Entada bean	Sep.	0	0	0	0	0	0	0	0	1	0	0	1
Macaranga nectar	Sep.	0	0	8	2	22	0	0	0	0	0	0	32
Insect larvae	Sep.	0	0	13	1	0	0	0	0	0	0	0	14
Total		29	93	100	142	246	194	117	42	37	20	1	1,021

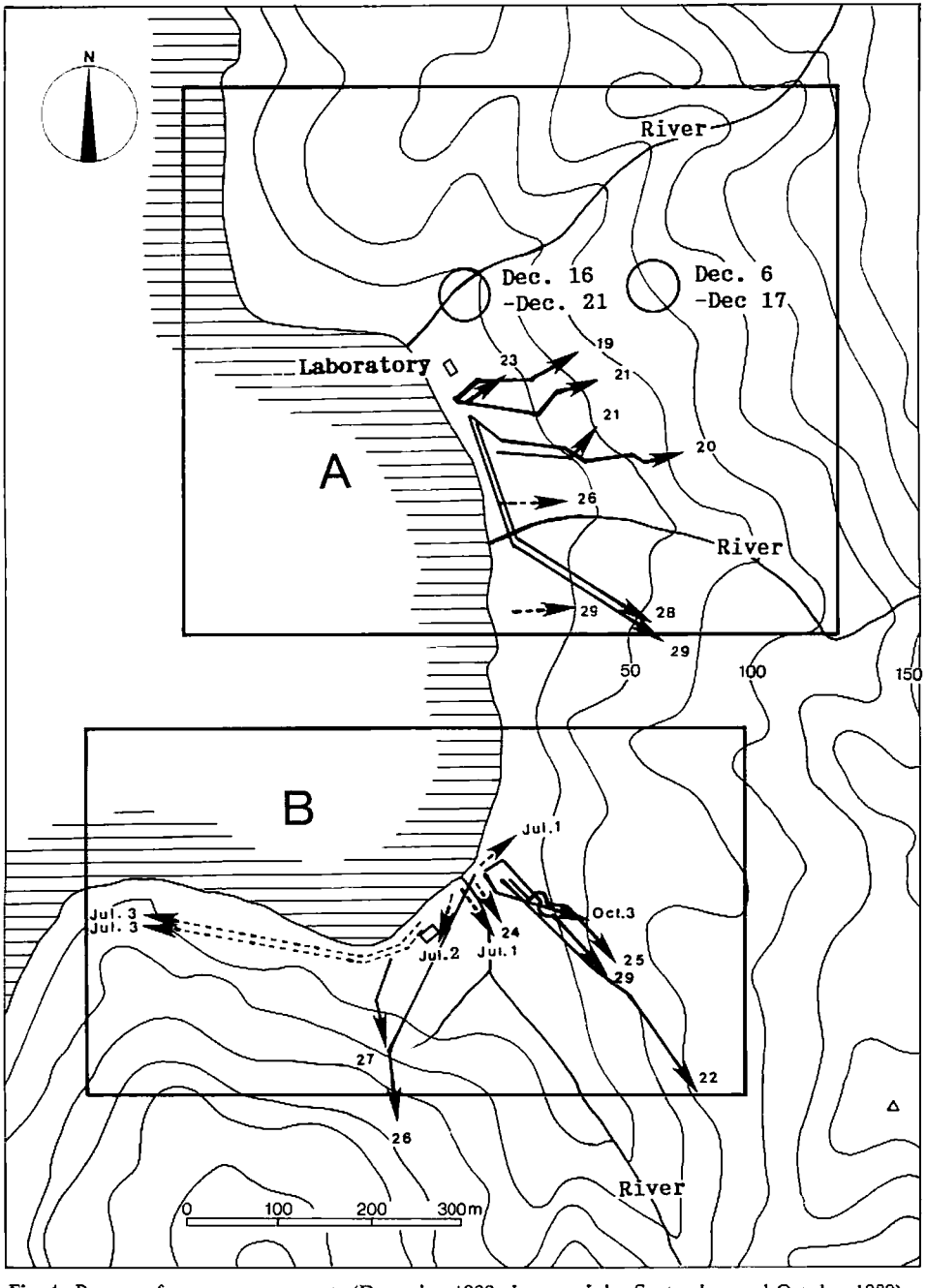

Fig. 4. Routes of aye-aye movements (December 1988, June to July, September and October 1989). ——→: June and July 1989; ⟶: September and October 1989; ◯: December 1988.

Table 4. Seasonal changes in aye-aye activity from December 1988 to October 1989.

Month	Feeding	Moving	Resting	Social behavior	Vocal communication	Unknown	Total
December	355(47.0)	355(47.0)	28(3.7)	0(0.0)	18(2.4)	0(0.0)	756(100.0)
June–July	142(31.1)	261(57.1)	47(10.3)	0(0.0)	2(0.4)	5(1.1)	457(100.0)
September	417(28.8)	753(52.1)	256(17.7)	9(0.6)	5(0.3)	6(0.4)	1,446(100.0)
October	109(43.4)	113(45.0)	22(8.8)	3(1.2)	4(1.6)	0(0.0)	251(100.0)
Total	1,023(35.2)	1,482(50.9)	353(12.1)	12(0.4)	29(1.0)	11(0.4)	2,910(100.0)

Upper: Observation units; Lower: Percentages.

feeding conditions (103 seconds, Iwano in press), because the value in the present study includes the searching time. All things considered, it can be said that the aye-aye consumes about one ramy nut every two minutes under natural conditions.

VI. Hourly Changes of Activity and Duration of Individual Activities

To observe the nocturnal activity of the aye-ayes, I waited at a place where a main food item of the season was present, where I could spot and follow the aye-ayes (Fig. 4).

In June, July, September and October 1989, aye-ayes were spotted in *A. bijuga* trees along the coast in the evening, feeding in the trees, and moving toward the mountainous region. Aye-ayes, after moving a while, frequently disappeared suddenly, which was probably because they hid in their nests or resting places. In fact, on October 3, 1989 I observed an aye-aye, after moving, entering its nest.

Such movements sometimes took place on the same routes. This suggests that an individual, after feeding at a frequented feeding site, returns to its resting place.

In general, aye-ayes used higher tree tops over 20 m above the ground for moving, but they occasionally descended to a height of 2 to 3 m above the ground and closer to the observers. It remains unclear whether these actions represented displays of threat or mere curiosity.

Aye-ayes moved about by a variety of methods including: traversing among the branches by holding on to twigs, swinging from one branch to another branch by holding onto the tips of branches (sometimes the animals move upside-down, hanging by their limbs), climbing up or down tree trunks using their claws, jumping from one branch to another, and sliding down a vine by hanging from their forelimbs (witnessed only once when tried by a young individual). During such movements, aye-ayes did not use their third digits for grasping the branches and the trunks. Movement on the ground was never observed.

A total of 2,910 observation units were recorded, of which 35.2% comprised feeding activity (Table 4). Feeding activity was comparatively high in October and December, while resting showed a decrease in those months (for the test of the difference between two proportions, see Appendix 1).

Table 5. Social contacts of aye-ayes observed in 1988 and 1989.

	Hour									Total
	18	19	20	21	22	23	0	1	2	
Contacts of 2 individuals										
Dec. 1988										
Duration	0	1	1	5	2	48	6	31	3	97
No. of occasion	0	1	1	4	2	5	2	3	1	19
Jun.–Jul. 1989										
Duration	0	0	0	0	4	0	0	0	0	4
No. of occasion	0	0	0	0	1	0	0	0	0	1
Sep.–Oct. 1989										
Duration	4	44	37	21	0	0	0	33	0	139
No. of occasion	4	3	4	1	0	0	0	1	0	13
Contacts of 3–4 individuals										
Dec. 1988										
Duration	0	6	0	0	43	5	11	20	0	85
No. of occasion	0	1	0	0	1	1	1	1	0	5
Sep.–Oct. 1989										
Duration	0	0	10	0	0	0	7	35	0	52
No. of occasion	0	0	1	0	0	0	1	1	0	3

V. Social Relations

1. Observation of More than One Individual in Close Proximity

In general, aye-ayes were observed alone. However, in all study periods, it was quite common to observe one aye-aye (four at maximum) active in the same vicinity (Table 5). "The same vicinity" means that the observer could see all the animals simultaneously, although they were sometimes separated by as much as 20 m. Aye-ayes can perceive other individuals from farther away than 20 m.

Close proximity of two individuals was observed for a total of 240 minutes or 8.3% of all periods during which the aye-ayes were observed to be active (2,910 minutes). Accordingly, the data on social activity totaled 12 minutes in duration, or about one twentieth of the periods at which proximity of two individuals was confirmed. The duration for which more than three individuals were observed in the same vicinity was 137 minutes (4.7%). Thus, more than one aye-aye was active in the same vicinity in about 13% of all the periods during which activity was observed.

The duration for which more than one aye-aye was observed at one place became shorter from June to July, which may be explained by the generally lowered activity of aye-ayes at that time.

In December (1988) and from June to July (1989), more than one aye-aye (four at maximum) was observed to feed on ramy or move within 20 m of each other. In those periods, however, even though aye-ayes approached to within 3 to 4 m of each other, they soon moved apart without displaying any notable social interaction during such contacts.

2. Social Behavior

From September to October (1989), contacts between different individuals occur-

red on 16 occasions and of them eight were associated with social behavior.

The social behavior observed during an encounter can be roughly classified into aggression over feeding places and interactions resembling courtship.

(1). Aggression over feeding places

Aggression over feeding places was observed twice on September 25 and September 29. The former case concerned a young female feeding on an *A. bijuga* tree. The female quarreled three times with another female approaching her, finally chasing away the challenger. Immediately after the fighting, the young female resumed feeding on the bark of the same *A. bijuga* despite the opponent's presence only 6 m away. In the latter case, a young male was eating ramy when another individual (sex unknown) approached, only to be chased away. There were a number of vocalizations consisting of high-pitched "Kwee-a" calls between the male and the approaching individual.

(2). Other interactions

Interactions suggestive of courtship were observed six times, of which three consisted of a series of actions involving four different individuals, two consisted of a female approaching a male and chasing after him (for five minutes in one case, and 33 minutes in the other), and in one case, the same two individuals were perched in a tree.

For example, at 20:05 hrs on September 20, a young male was feeding on an *A. bijuga*, when a young female with a blind left eye approached. The two approached each other suddenly, and immediately parted. The two repeated these behaviors at 20:09 and 20:12 hrs. They did not use their hands nor bite each other. I could not determine which one was dominant. During this activity, they remained within a distance of 3 m to each other. Later, the two moved slowly keeping a distance of less than 10 m from each other.

The same young male and female were perched in a tree of *M. cuspidata* 6 m apart from each other. The male left for a while, returned to the young female at 20:21 hrs, and, after making a quick approach, stayed away from her. At 20:34 hrs, the young male left the female, who was now resting. Later, the female intermittently moved and rested. In the meantime, "Kwee-a" vocalizations were heard six times until 21:23 hrs from a place 15–30 m away. However, the female remained unresponsive to them.

At 21:23 hrs, a young male (it was unclear whether this was the same individual as above) appeared anew. At 21:25 hrs, the male circled around the female at a distance of 4 m, and then approached her to a distance of 1 m. At 21:32 hrs, the male followed the female, who was now moving, at a distance of 4–6 m. At 21:44 hrs, the two were observed resting at a distance of 4 m from each other. At 21:48 hrs, the female was observed to be absent and the male began to eat *M. cuspidata* flowers.

The next example also concerns the female with the blind left eye and a young male.

At 0:54 hrs on October 4, while the female was engaged in feeding on ramy, a young male approached, rested at a distance of 10 m from her and engaged in self-grooming. At 0:58 hrs, the two vocalized, and then the female attacked quickly and retreated. Later, the two rested until 1:02 hrs at a distance of 1.5–3 m from

each other. They disappeared for a while, but their calls were heard 12 times between 1:12 and 1:25 hrs. They appeared again and attacked each other at 1:27 hrs again at 1:28 hrs. At 1:34 hrs, the female started to move away, and soon thereafter, the male also moved off, and they disappeared.

3. Vocalization

Throughout all seasons, aye-ayes generate high-pitched calls sounding like "Nee-a", and they exchange these calls with each other (Fig. 5). This call has a frequency of 3 KHz and is 80 msec in duration (analyzed by Dr. N. Masataka using a digital sonagraph 7800, KAY Electronics Co.).

This call corresponds to the one Petter (1977) described as a "Cree" sound, which was exchanged between a mother and its baby in the wild. Petter & Charles-Dominique (1979) did not mention this wave form.

These vocalizations could be heard in various situations, and, in particular, were frequently heard in December 1988. At that time, a young individual, emitting such calls repeatedly, turned round and round the same ramy tree. From 8:00 to 9:00 hrs on December 19, the interval between the calls was 9–16 seconds. At 1:00 hrs on December 20, the same individual (so assumed), which had continuous-

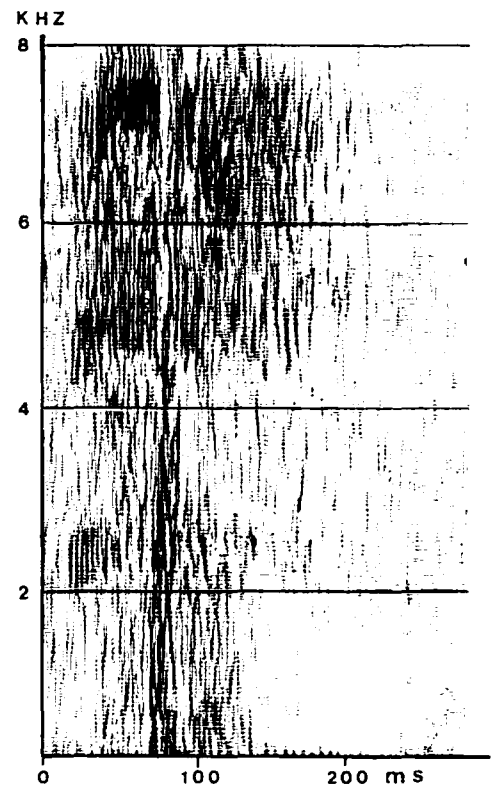

Fig. 5. Sonogram of the aye-aye's call.

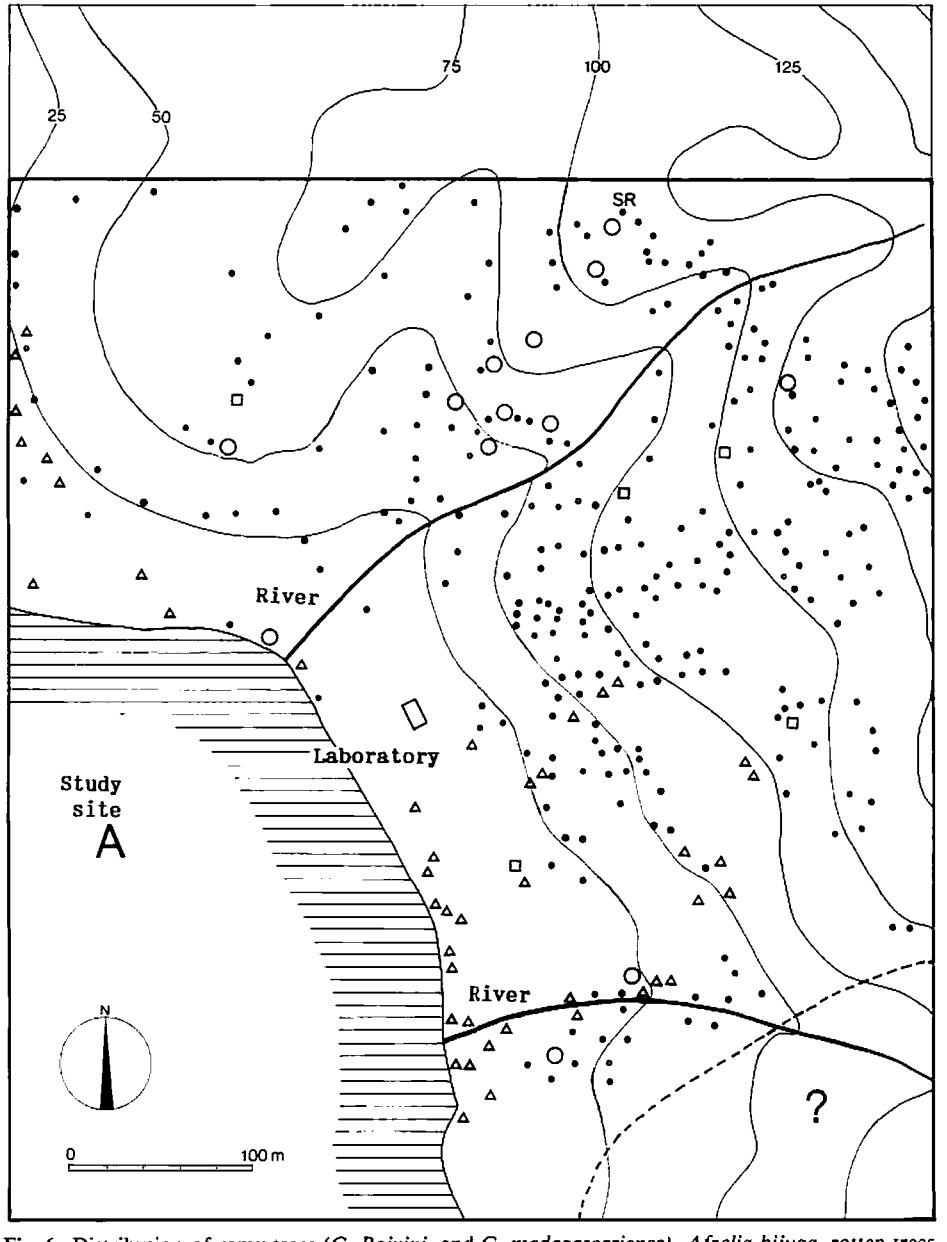

Fig. 6. Distribution of ramy trees (*C. Boivini*, and *C. madagascariense*), *Afzelia bijuga*, rotten trees, and aye-aye nests in Study Area A.
●: *C. Boivini*; SR: *C. madagascariense*; △: *Afzelia bijuga*; ○: Rotten tree; □: aye-aye nests.
* Total numbers counted: 281 for ramy, 46 for *Afzelia bijuga*, 13 for rotten trees and 5 for nests (June 20, 1989).

ly emitted the calls, encountered another bigger individual, but they soon left each other. During this period, aye-ayes were not observed to feed on ramy. Probably in this case, the calls were exchanged between the young animal and its parent, while in the cases described above (occurring from September to October 1989), male-female pairs communicated with each other by vocalizing.

A second kind of vocalization was heard, probably meant as a threat to the observers. On July 1, when a young female was feeding on the bark of No. 2 *A. bijuga* tree along the coast, an adult male appeared on No. 1 *A. bijuga* tree (about 20 m from No. 2) and emitted a low, resonating "Kuftt, kuftt" sounding, probably as a threat to the observers. This individual repeated the same call and moved into the forest, while the female continued eating the bark as before. At 21:30 hrs on July 3, a young male on No. 1 *A. bijuga* tree vocalized in the same way toward the observers.

VI. On the Ramy Nuts

1. Seasonal Changes in the Fruiting of Ramy

I undertook surveys on the distribution of ramy and its fruiting in Study Area A in December 1988 and June 1989 (Fig.6).

In December, I studied 185 ramy trees in Study Area A, and found that 41 (22.2%) bore fruit, and in June found that 16 of 281 ramy trees (5.7%) bore fruit, one of which was *C. madagascariense*. I studied 23 ramy trees in Study Area B in September, and found that five (21.7%) developed fruit. In addition, at least three of the ramy trees that had born fruit in December were still in fruit in June of the next year.

For further confirmation of this point I launched a survey from June 1989 to October 1990 in which 47 ramy trees, including one *C. madagascariense*, were sampled for their fruiting condition twice a month (Appendix 2). According to this survey, the fruiting season of *C. Boivini* started in January and lasted until October (Table 6). In November, December and January, they blossomed.

The single *C. madagascariense* chosen as a study subject had many fruits from January to August. I could see only two nuts in September, indicating that it practically ceased to bear fruit. Its fruiting season was similar to *C. Boivini*.

Contrary to the result of my phenological survey, in December 1984 and 1988

Table 6. Number of fruiting ramy trees (*Canarium Boivini*) among 46 samples from June 1989 to June 1990.

	1989							1990					
	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	Jun.
Fruit													
Many	6	6	6	5	2	0	0	11	11	11	11	11	9
Few	9	4	3	4	2	2	1	1	4	4	2	2	3
Total	15	10	9	9	7	4	1	1	15	15	13	13	12
Percent.	32.6	21.7	19.6	19.6	15.2	8.7	2.2	2.2	32.6	32.6	28.3	28.3	26.1

Many fruit: More than 10 nuts observed.
Few fruit: Less than 9 nuts observed.
Percentage: To total (46) samples.

Table 7. Nutritional composition and calorie contents of the ramy nut (per 100 g edible portion).

Component	Percentage	Method for analysis
Water	7.3	Drying by heating under normal pressure
Protein	13.3	Kjeldahl method
Lipid	54.2	Soxhlet's extraction method
Ash	4.4	Direct method
Carbohydrate	20.8	100−(Water+Protein+Lipid+Ash)
Energy	584 kcal/100g	

there were many ramy fruits in those sample trees. Therefore, I can say that *C. Boivini* bears fruit all year round in Nosy Mangabe.

2. Nutritional Analysis of Ramy Nuts

Nutritional analysis of the edible portion of a ramy nut revealed that it contained a high fraction of lipids and has a high energy content (584 kcal/100g) (Table 7. Analyzed by Japan Food Analysis Center). The conversion factors for calories were 3.47 for protein, 8.37 for lipid and 4.07 for carbohydrate. This nutritional composition and energy content is equal to the walnut, the dry content of which has an energy of 673 kcal/100g (Resources Council, Science and Technology Agency, Japan, 1985).

The edible portion of a ramy nut weighs about 0.75 g, which corresponds to 4.38 kcal in terms of energy.

DISCUSSION

I. Correlation between Distribution of the Aye-Aye and That of Ramy

The distribution of the aye-aye and those of *Canarium* spp. overlapped in the eastern coast and in the central highland of Madagascar. In the eastern coastal region, two species of ramy coexist with different fruiting seasons. *C. Boivini* bears fruit almost all-year, while *C. madagascariense* has its fruiting season between May and September (Cabanis et al., 1970). Thus, it can be said that the tropical forest in the eastern coastal region would be advantageous for the aye-aye to utilize ramy nuts as a staple food.

Of the ramy (genus, *Canarium*; family, Burseraceae) three species are known in Madagascar. The distribution of the third species, *C. pulchrebracteatum* Guill, which occurs in the south-western part (Perrier, 1946), is a topic for future study, since the extinct giant aye-aye (*D. robusta*) was distributed in a similar locality (Lamberton, 1934; MacPhee & Raholimavo, 1988).

II. Food Selection by Aye-Ayes

In 1985, Pollock et al. reported that aye-ayes fed on the bark of *A. bijuga* trees. From their findings of bark deformed by parasitism, bitten off by aye-ayes, these investigators suggested either that aye-ayes consume the sap from the tree, or feed on

insect larvae and frogs inhabiting the bark. According to our observations, however, aye-ayes did not eat insect larvae nor frogs in the bark of *A. bijuga* trees but preferentially fed on the fragrant parts of the cambial layer beneath the parasitically induced outgrowths of *A. bijuga* bark.

The feeding habits of aye-ayes are characterized by the fact that they ignore plant shoots and foliage, and other food items which are important in the diets of other prosimian groups living in the same area.

Whether the aye-aye can subsist solely on the bark of *A. bijuga* is a question to be dealt with in the future. For *A. bijuga* to sufficiently nourish the aye-aye it is necessary that its bark have sufficient energy content. The facts that the aye-aye feeds only on the bark deformed by parasitism and not on the intact bark, and that *A. bijuga* trees are only distributed along the coastal region, suggest that *A. bijuga* bark forms a supplementary food item peculiar to the coastal region.

III. Can Ramy Provide Sufficient Nourishment for the Aye-Aye?

In the ecological survey continued with some interruptions from December 1988 until September/October 1989, I found that aye-ayes largely depended on ramy, supporting my hypothesis that the ramy forms the staple food of the aye-aye. But it remains to be determined whether the aye-aye can actually subsist on ramy nuts alone.

1. Estimation from the Energy Content of the Ramy Nut

The energy contained in the albumen of a ramy nut the aye-aye habitually eats is rather high at 584 kcal/100g. As the content of one ramy nut is 0.75 g, a ramy nut has a total energy of 4.38 kcal on average. The quantity of nuts an aye-aye consumes in a night can only be estimated at, but, provided that an aye-aye is engaged in feeding for about two hours a night (this may be a rather low estimate, because more than 31.1 percent of activity record in the night, about three hours, was calculated as feeding) consuming one nut every two minutes, it consumes 60 nuts per night, resulting in a total energy intake of 262.8 kcal. Since a macaque weighing 4.2 kg has been estimated to have a basal metabolic rate of 207 kcal (Benedict, 1938 cited in Kleiber, 1975), the above figure appears to be sufficient for sustaining an aye-aye with a weight of about 3 kg, and the aye-aye may have the comparatively low metabolic rate that is found in other prosimians (Müller, 1985).

In the survey carried out in December 1984, I found that aye-ayes continuously fed on ramy nuts for almost three and a half hours, resulting in ingestion of a total energy of 459.9 kcal. This allows aye-ayes to enjoy a high energy intake during seasons of ramy nut abundance. During such periods, the aye-aye can build up fat deposits within the body, but it remains to be confirmed whether this fat is sufficient to sustain the aye-aye through other periods lasting almost half a year when ramy nuts become less available. The answer to this question awaits a detailed nutritional study.

2. Estimate of the Aye-Aye's Population at the Nosy Mangabe Special Reserve

The ramy trees in the study area have an average DBH of 107.7 cm (N=23;

S.D., 42.7; range, 45.0–166.0 cm). While some trees have larger diameters, their buttress roots are so well-developed that it was difficult to measure the diameter. These trees reach a height of over 20 m, making it difficult to estimate how much fruit such a tree bears annually on average. As a trial, however, an estimate was made on a tree (No. 15, 14.5 cm DBH), of 3,000. Provided that one aye-aye consumes 60 ramy nuts per night, one ramy tree can provide 50 "daily rations." The Study Area A (about 20 ha) has a total of 281 ramy trees within its confines, and the ramy trees bearing fruits in December amounted to 22.2% of the sample examined (185). These trees produce 3,115 "daily rations," which, when divided by 365 (days per year), gives 8.53 as the number of aye-ayes that can be sustained by those trees in Study Area A. These figures give 2.34 ha (20 ha/8.5 individuals) as an activity area per aye-aye, which corresponds to a density of 42.7/km^2. If this density is occurred over the whole 5.2 km^2 of the Nosy Mangabe Special Reserve, 9 value of 222.2 is obtained as the total population of the aye-ayes which could be sustained by this area.

There are, in addition, a number of factors limiting the aye-aye's population: the Nosy Mangabe area also serves as the habitat for *Varecia variegata variegata* and *Lemur fulvus albifrons* which compete with aye-ayes for ramy nuts (Iwano, 1989). Furthermore, ramy nuts are not available throughout the year, and ramy nuts are not evenly distributed over the whole area. This issue would be moot if aye-ayes could store ramy nuts in some way or another. In fact, the aye-aye in captivity at Botanical and Zoological Park in Tsimbazaza was observed to deposit coconuts in a secret cache. In short, from the nutritional standpoint, the above figures suggest that the Nosy Mangabe Special Reserve has an ample capacity for sustaining a considerable number of aye-ayes (the energy balance at periods when ramy fruits are comparatively scarce is ignored for purposes of this discussion).

Future discussions of aye-aye ecology should be facilitated by using my figures as references, especially when considering activity areas of aye-ayes and their population density.

IV. Can Wood-Boring Insect Larvae Provide Sufficient Nourishment for Aye-Ayes?

In feeding on the bark of *A. bijuga* and insect larvae, as already noted by Petter (1977), it is unlikely that the energy expended in feeding can be made up for by the energy actually ingested. Aye-ayes, however, seemed to feed on insect larvae throughout the survey periods as judged from their feeding marks.

In June 1986, I identified one tooth mark left on the surface of a dead tree in isolation. To reach that tree, the aye-aye must have walked on the ground, an unusual behavior for this arboreal creature. This indicates a remarkably intense predilection of aye-ayes toward wood-boring larvae. Such favorite food articles would be eaten throughout the year; that is, whenever available, aye-ayes feed on them.

The observation units during which aye-ayes were observed to feed on wood-boring larvae accounted for only 1.4% of all observation units related with feeding activity, suggesting that such a low intake of larvae, even if larvae have a high

energy content per unit weight, would not be sufficient for sustaining an aye-aye.

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Appendix 1. Statistical tests of the difference between months for three activities.

Feeding

	June/July	September	October
December	5451	8.461	0.973
	$p<0.01$	$p<0.01$	$p>0.05$
June/July	–	0.914	3.287
		$p<0.05$	$p<0.01$
September	–	–	4.613
			$p<0.01$

Moving

	June/July	September	October
December	4.611	9.307	3.198
	$p<0.01$	$p<0.01$	$p<0.01$
June/July	–	3.779	0.652
		$p<0.01$	$p>0.05$
September	–	–	3.53
			$p<0.01$

Resting

	June/July	September	October
December	3.428	2.280	0.533
	$p<0.01$	$p<0.05$	$p>0.05$
June/July	–	1.881	3.083
		$p>0.05$	$p<0.01$
September	–	–	2.064
			$p<0.05$

Appendix 2. Phenology of the ramy at Nosy Mangabe.

Year		1989												
Month		June	July		August		September		October		November		December	
Date		15	15	25	15	25	15	25	15	25	15	25	15	25
C.B.	1	f	F	F	F	F	F	F	F	F	F	F	B	Fl
	2	No	No	No	No	No	No	No	No	No	No	No	Fl	Fl
	3	No	No	No	No	No	No	No	No	No	No	No	Fl	Fl
	4	No	No	No	No	No	No	No	No	No	No	No	No	Fl
	5	O	O	O	O	O	O	O	O	O	No	No	Fl	Fl
	6	No	No	No	No	No	No	No	No	No	No	No	No	No
	7	No	No	No	No	No	No	No	No	No	No	B	Fl	Fl
	8	No	No	No	No	No	No	No	No	No	No	No	No	No
	9	No	No	No	No	No	No	No	No	No	No	No	Fl	Fl
	10	No	No	No	No	No	No	No	No	O	O	B	Fl	Fl
	11	No	No	No	No	No	No	No	No	No	No	B	Fl	Fl
	12	No	No	No	No	No	No	No	No	No	No	O	No	Fl
	13	No	No	No	No	No	No	No	No	No	No	No	No	No
	14	No	No	No	No	No	No	No	No	No	No	No	No	No
	15	No	No	No	No	No	No	No	No	O	O	No	Fl	Fl
	16	No	No	No	No	No	No	No	No	O	O	No	Fl	Fl
	17	F	F	F	F	F	F	F	F	F	F	F	Fl	Fl
	18	No	No	No	No	No	No	No	No	No	No	No	No	No
	19	F	F	F	F	f	f	f	No	No	No	No	No	No
	20	F	No	No	No	No	No	No	No	No	No	No	No	No
	21	No	No	No	No	No	No	No	No	No	No	No	No	No
	22	No	No	No	No	No	No	No	No	O	No	No	No	No
	23	No	No	No	No	No	No	No	No	O	No	B	Fl	Fl
	24	No	No	No	No	No	No	No	No	O	No	Fl	Fl	Fl
	25	No	No	No	No	No	No	No	No	O	No	No	B	Fl
	26	No	No	No	No	No	No	No	No	O	No	No	No	No
	27	No	No	No	No	No	No	No	No	O	No	B	Fl	Fl
	28	F	F	F	F	F	F	F	F	F	No	B	Fl	Fl
	29	No	No	No	No	No	No	No	No	No	No	No	No	No
	30	F	F	F	F	F	F	F	F	f	f	No	No	No
	31	No	No	No	No	No	No	No	No	No	No	B	Fl	Fl
	32	f	f	f	f	f	f	f	f	f	No	No	B	Fl
	33	No	No	No	No	No	No	No	No	No	No	B	B	Fl
	34	No	No	No	No	No	No	No	No	No	No	No	No	No
	35	No	No	No	No	No	No	No	No	No	No	No	No	No
	36	f	f	f	No	No	No	No	No	No	No	B	Fl	Fl
	37	No	No	No	No	No	No	No	No	No	No	B	Fl	Fl
	38	f	f	f	f	f	f	f	f	f	No	No	No	No
	39	No	No	No	No	No	No	No	No	No	No	No	No	No
	40	No	No	No	No	No	No	No	No	No	No	No	No	No
	41	F	F	F	F	F	F	F	F	F	f	f	f	f
	42	f	No	No	No	No	No	No	No	O	No	No	B	Fl
	43	f	No	No	No	No	No	No	No	O	No	No	B	Fl
	44	f	No	No	No	No	No	No	No	O	No	No	No	No
	45	f	No	No	No	No	No	No	O	O	No	No	No	No
	46	f	f	f	f	f	f	f	No	No	No	No	No	No
C.m.	1	F	f	f	f	f	f	No	No	No	No	No	No	No

Year		1990											
Month		January		February		March		April		May		June	
Date		15	25	15	25	15	25	15	25	15	25	15	25
C.B.	1	Fl	F	F	F	F	F	F	F	F	F	F	F
	2	Fl	No	No	No	No	No	No	No	No	No	No	No
	3	Fl	No	No	No	No	No	No	No	No	No	No	No
	4	Fl	F	F	F	F	F	F	F	F	F	f	f
	5	Fl	No	No	No	No	No	No	No	No	No	No	No
	6	No	No	No	No	No	No	No	No	No	No	f	f
	7	Fl	No	No	No	No	No	No	No	No	No	No	No
	8	No	No	No	No	No	No	No	No	No	No	No	No
	9	Fl	F	F	F	F	F	F	F	F	F	F	F
	10	Fl	No	No	No	No	No	No	No	No	No	No	No
	11	Fl	F	F	F	F	F	F	F	F	F	F	F
	12	Fl	F	F	F	F	F	F	F	F	F	F	F
	13	No	No	No	No	No	No	No	No	No	No	No	No
	14	No	No	No	No	No	No	No	No	No	No	No	No
	15	Fl	No	No	No	No	No	No	No	No	No	No	No
	16	Fl	No	No	No	No	No	No	No	No	No	No	No
	17	Fl	F	F	F	F	F	F	F	F	F	F	F
	18	No	No	No	No	No	No	No	No	No	No	No	No
	19	No	No	No	No	No	No	No	No	No	No	No	No
	20	No	No	No	No	No	No	No	No	No	No	No	No
	21	No	No	No	No	No	No	No	No	No	No	No	No
	22	No	No	No	No	No	No	No	No	No	No	No	No
	23	Fl	No	No	No	No	No	No	No	No	No	No	No
	24	Fl	No	No	No	No	No	No	No	No	No	No	No
	25	Fl	F	F	F	F	F	F	F	F	F	F	F
	26	Fl	f	f	f	f	f	No	No	No	No	No	No
	27	Fl	No	No	No	No	No	No	No	No	No	No	No
	28	Fl	No	No	No	No	No	No	No	No	No	No	No
	29	Fl	F	F	F	F	F	F	F	F	F	No	No
	30	No	No	No	No	No	No	No	No	No	No	f	f
	31	Fl	No	No	No	No	No	No	No	No	No	No	No
	32	Fl	f	f	f	f	f	f	f	f	f	No	No
	33	Fl	No	No	No	No	No	No	No	No	No	No	No
	34	No	No	No	No	No	No	No	No	No	No	No	No
	35	No	No	No	No	No	No	No	No	No	No	No	No
	36	Fl	No	No	No	No	No	No	No	No	No	No	No
	37	Fl	No	No	No	No	No	No	No	No	No	No	No
	38	No	No	No	No	No	No	No	No	No	No	No	No
	39	No	No	No	No	No	No	No	No	No	No	No	No
	40	No	No	No	No	No	No	No	No	No	No	No	No
	41	Fl	F	F	F	F	F	F	F	F	F	F	F
	42	Fl	F	F	F	F	F	F	F	F	F	F	F
	43	Fl	F	F	F	F	F	F	F	F	F	F	F
	44	Fl	f	f	f	f	f	No	No	No	No	No	No
	45	No	No	No	No	No	No	No	No	No	No	No	No
	46	f	f	f	f	f	f	f	f	f	f	No	No
C.m.	1	F	F	F	F	F	F	F	F	F	F	F	F

C.B.; *Canarium Boivini; C.m.*: *Canarium madagascariense.*
No: No fruit; B: Bud; F: Many fruit; O: Old leaves; f: Little fruit; Fl: Flowering